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Mycorrhizal dynamics during forest tree development

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Introduction

The wide variety of necrotrophic, saprotrophic and biotrophic fungi living within the forest habitat form a dynamic interacting community in which niches are both lost and gained and the composition of the community regularly changes. We know little, however, of the structure of these changing communities or the actual mechanisms whereby one species replaces another (Frankland, 1981).

One of the most important groups of fungi within the forest flora are the mycorrhizal fungi. They are important in nutrient cycling as, in conjunction with their host plant, they act as a sink for mineral ions derived from within the soil. They also produce vitamins and hormones which appear to increase root size and longevity (Slankis, 1973). Mycorrhizal fungi, in turn, depend largely on their hosts for their energy and carbon requirements. Thus mycorrhizas broadly function as a mutualistic symbiotic biotrophy between a fungus and a higher plant (Lewis, 1973).

Although mycorrhizas are a key link in nutrient and energy cycling within the forest ecosystem, we know little about the changes in mycorrhizal species composition or function as forests develop and reach a climax, nor of the processes which may control or affect such changes.

During the development and growth of natural and planted forests, a number of changes in vegetation occur which, in turn, affect the physico-chemical attributes of the soil ecosystem in which the mycorrhizas are active. Thus, as forest trees age, the resources available to the mycorrhizas and their host plants will alter (Fig. 5.1). Plant, animal and probably fungal species diversities increase as trees age, and then decline following canopy closure and the development of a climax community (Usher & Parr, 1977). The resource quality available to the decomposer community declines with the decline of understorey herbaceous vegetation (Ford & Newbould, 1977; Cromack, 1981) as more lignin and polyphenols become incorporated into the litter. As a consequence, litter residence time increases, organic matter accumulates and organisms tend to adopt '*K*-' rather than '*r*-' strategies (Southwood, 1977; Gerson & Chet, 1981; Heal & Ineson, 1984; Heal & Dighton, 1985; see also Rayner, Watling & Frankland: Chapter 1). As trees become larger it is hypothesised that their demand for nutrients from soil decreases as internal recycling of nutrient within the tree becomes more efficient (Miller, 1979; Miller *et al.* 1979). These changes are important in terms of the rate of release of labile nutrients available to the mycorrhizal roots and the tree's nutrient demand. It is also envisaged that the amount of carbohydrate available to support a mycorrhizal fungal symbiont might differ with tree size/age, with small trees having limited supplies and supporting fungi with limited carbohydrate demands, while larger trees support carbohydrate-demanding fungi. It is probable, therefore, that the stage of development of the ecosystem will strongly influence the resources available to mycorrhizal fungi.

Thus it is expected that the species of fungi forming mycorrhizas with a tree 40 years old will differ from those associated with saplings. Nevertheless, the concept of 'mycorrhizal succession' is only now being unravelled as a result of several pieces of circumstantial evidence. In theory, fungal successions are not uncommon (Frankland, 1981) but until recently there has been scant information concerning changes in a mycorrhizal flora with stand development. As a result, the purpose of this chapter is to document the current information regarding changes in the ectomycorrhizal flora of temperate forests, which is chiefly agaricoid, and to highlight some of the processes which might be responsible for this mycorrhizal succession.

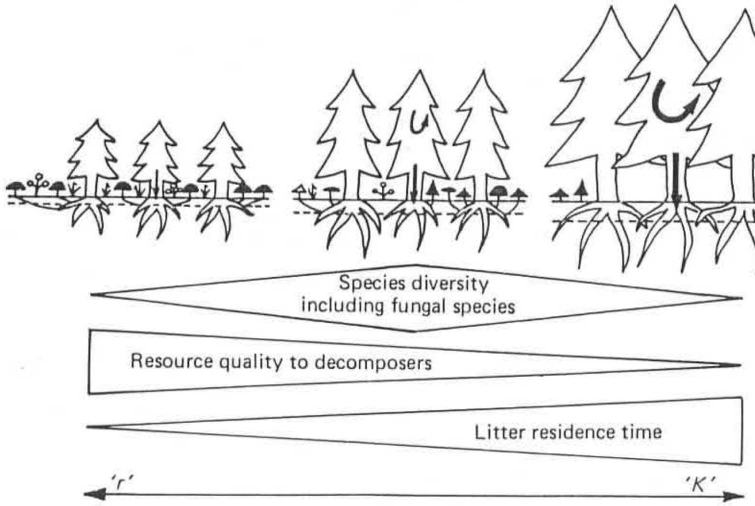
Species diversity including fungal species
Resource quality to decomposers
Litter residence time
'r'
'K'

Fig. 5.1. Diagrammatic representation of forest succession indicating growth of trees, shading of ground flora and changes in ectomycorrhizal composition with stand development. Changes in resources are indicated; arrows within trees represent the hypothesised increase in internal recycling of nutrients in the tree and possible changes in carbohydrate supply to the root system with stand age. These concepts and the change from '*r*' to '*K*' attributes of organisms are discussed in the text.

Changes in mycorrhizal dynamics

Evidence from fruit body observations

Terrestrial plant communities tend to be dominated by either endomycorrhizal or ectomycorrhizal plants (Moser, 1967). During ecosystem succession to climax forest in northern temperate regions the fungal associates of higher plants change from endo- or vesicular-arbuscular mycorrhizas in herbaceous and scrub communities to ectomycorrhizas associated with trees (Rose, 1980). The ectomycorrhizal fungi associated with most coniferous species and many angiosperm trees belong to the Basidiomycotina, Zygomycotina and Ascomycotina. It is estimated that over 2000 fungal species are potential ectomycorrhizal symbionts (Trappe, 1962, 1977). Most of these species have been identified by fruit body characteristics e.g. toadstools and earthballs, which they produce each autumn. The host–fungus specificity is varied, birch (*Betula* spp.), for example, being associated with a number of fungal genera including *Amanita*, *Boletus*, *Cantharellus*, *Cortinarius*, *Hebeloma*, *Inocybe*, *Laccaria*, *Leccinum*, *Paxillus*, *Russula*, *Scleroderma* and *Tricholoma* (Trappe, 1962; Watling, 1973; Pegler, 1981). Many of these fungi, however, are not host-specific and are also associated with coniferous and other deciduous trees. Some fungi, e.g. *Suillus* and *Rhizopogon*, associate almost exclusively with the Pinaceae, and some tree species such as alder (*Alnus* spp.) have a restricted mycorrhizal flora (Molina, 1979). Mixed forests tend to be more diverse in fungal composition than pure stands (Mosse, Stribley & Le Tacon, 1981).

Most lists showing the association of fruit bodies of sheathing ectomycorrhizas have paid little attention to soil conditions, climate, and age and size of tree. We can see, however, that superimposed upon the tree/fungus heterogeneity there is a temporal shift in the species composition of the mycorrhizal flora of a monospecific tree stand as the trees age. In a stand

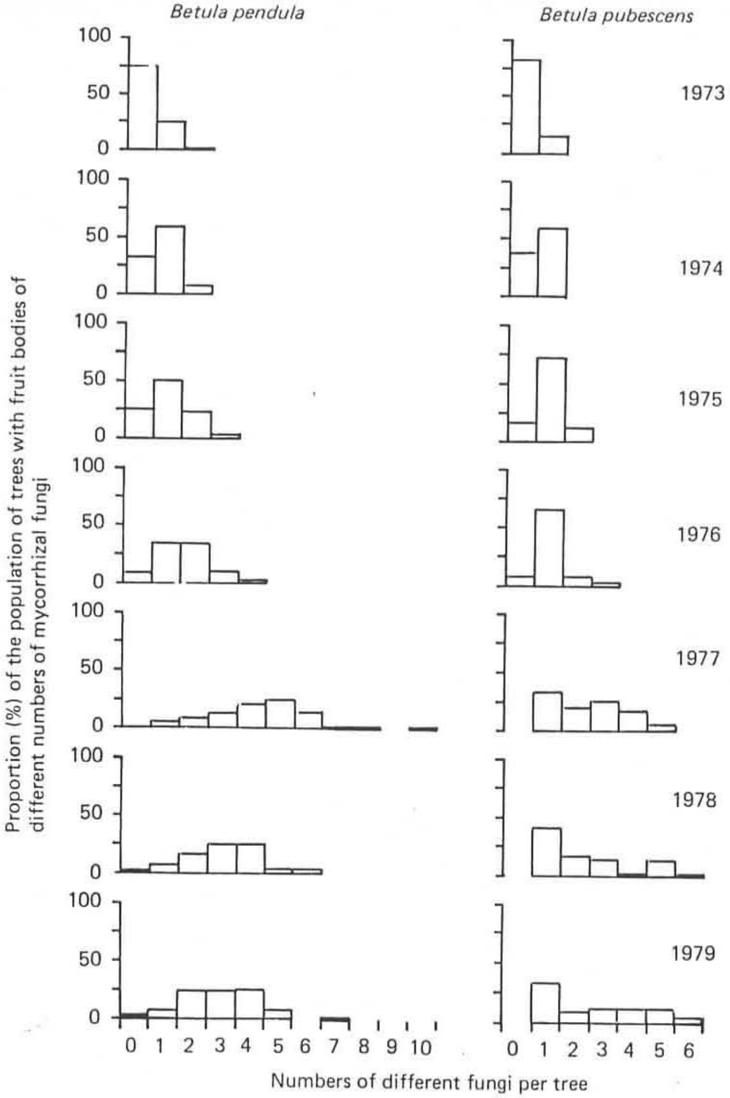

Fig. 5.2. Number of trees (expressed as a proportion of the total trees) under which different numbers of mycorrhizal fruit body species appear in successive years after planting saplings of *Betula pendula* and *B. pubescens* in 1971. (After Mason *et al.* 1982.)

of birches of *Betula pendula* and *B. pubescens*, clear evidence has been obtained of a sequence of ectomycorrhizal fruit bodies in both time and space (Mason *et al.*, 1983). *Hebeloma crustuliniforme* and *Laccaria tortilis* were observed within 2 years of planting; *Inocybe lanuginella* and *Lactarius pubescens* appeared in year 4, while species of *Cortinarius* and *Leccinum* were recorded in year 6 and *Russula* spp. in year 10 (Last *et al.*, 1983). Similar data are present in the literature for coniferous species where *Thelephora terrestris*, *Hebeloma* spp., *Laccaria* spp. and *Inocybe* spp. are associated with young trees (Trappe & Strand, 1969; Chu-Chou, 1979; Chu-Chou & Grace, 1981, 1983). Fungi often associated with nursery soils, e.g. *Thelephora terrestris* and *Hebeloma crustuliniforme*, may be lost at outplanting (Mosse *et al.*, 1981) but others, including *Laccaria* spp., may be found in both young and mature stands. Chu-Chou (1979) associated fruit bodies of *Suillus* and *Inocybe* species with stands of *Pinus radiata* 5 or more years old, while *Amanita muscaria* toadstools were only found in plantations at least 10 years old. Distinct successions have also been reported from ageing stands of Norway spruce in the French Jura (Mosse *et al.*, 1981).

Not only do the dominant species of mycorrhizal fungi alter with tree age, but the species diversity also changes. Last *et al.* (1983) indicated that on a brown earth the number of fungal species associated with *Betula pendula* and *B. pubescens* increased from four species in year 3 to nearly 30 species in year 10, with a consistently greater variety of fungi associated with *B. pendula* (Mason *et al.*, 1982) (Fig. 5.2). In a survey of fruit body production of fungi under *Pinus contorta* of different ages planted on peat, clear changes in fungal diversity with stand development could be seen with *Lactarius rufus* being dominant under smaller trees, a diverse group of fungi including *Laccaria*, *Inocybe longicystis* and *Cortinarius* species occurring at canopy closure, and a reduced diversity of mycorrhizal fungi dominated by *Russula emetica* in the well-developed sites, after canopy closure (Fig. 5.3). The changes in species diversity of the most commonly occurring fruit bodies with stand age is indicated in Fig. 5.3, the reduction of diversity in older stands agrees with data from root assessment in 250-year-old Douglas fir/larch (*Pseudotsuga menziesii*/*Larix*) forests (Harvey, Larsen & Jurgensen, 1976) indicating that fir and larch were each associated with a single dominant mycorrhizal fungus, *Russula brevipes* and *Suillus cavipes*, respectively.

In summary it is observed that some mycorrhizal fungi (e.g. *Hebeloma*, *Laccaria* and *Inocybe*) are characteristic of young stands, whereas others (e.g. *Cortinarius*, *Russula* and *Amanita*) are associated with older stands.

The concept of mycorrhizal succession based on fruit body observation is given credence by the close relation between fruit bodies and their own mycorrhizal type occurring on roots, observed by Warcup (see Mason *et al.*, 1982). The sequence of fungi can, however, be modified by soil type and environmental factors; *Paxillus involutus* was dominant on young birch growing in coal spoil (Last, unpublished) although it was not observed on young trees growing in a brown earth soil (Mason *et al.*, 1982), indicating possible selection for adverse environmental conditions, i.e. adversity strategy (Southwood, 1977) or stress-tolerant (*S*) strategy (Grime, 1979).

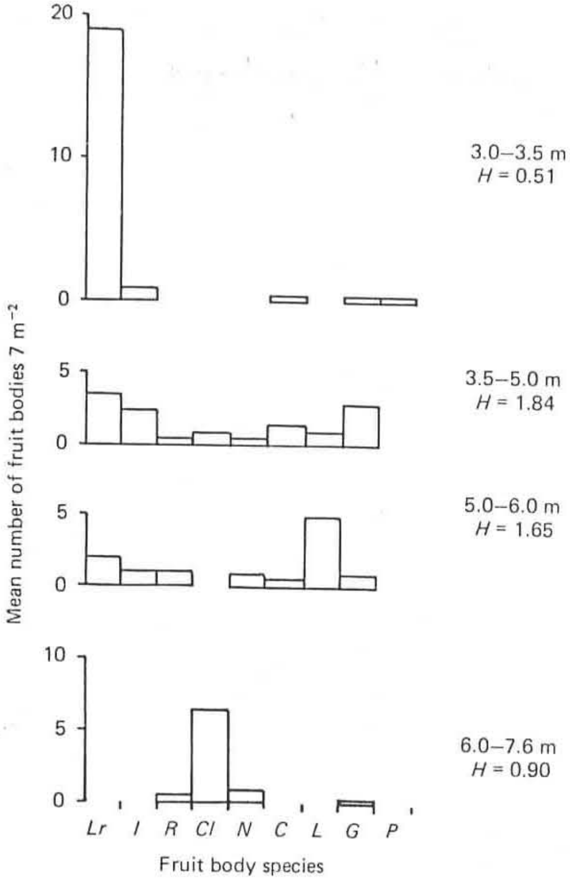

Fig. 5.3. Changes in the populations of fungal fruit bodies occurring under *Pinus contorta* stands at different stages in stand development (height classes) on peat in northern England. The *H*-value is the Shannon Weaver species diversity index. (*Lr* = *Lactarius rufus*; *I* = *Inocybe longicystis*; *R* = *Russula emetica*; *Cl* = *Clitocybe* sp.; *N* = *Nolanea cetrata*; *C* = *Cortinarius* sp.; *L* = *Laccaria* sp.; *G* = *Galerina* sp.; *P* = *Paxillus involutus*.)

Evidence from mycorrhizas

More definitive evidence for an age-related succession of mycorrhizal fungi has been presented by Deacon, Donaldson & Last (1983) who examined the distribution of mycorrhizas in soil cores taken at 0.25-m intervals from the base of an 8-year-old *Betula pubescens*. *Hebeloma*-type mycorrhizas were most frequent in the outer sampling positions on the newest part of the root system, while *Leccinum*-type mycorrhizas were found mostly in the inner sampling positions. *Leccinum* species are associated with later stages of the succession in contrast to *Hebeloma*, an 'early-stage' fungus. *Lactarius*-type mycorrhizas were found in all positions, although their frequency 'peaked' in the middle samples (Fig. 5.4). Evidence of this nature strongly supports the concept of mycorrhizal succession as observed by the pattern of fruit bodies with changes in tree age. On roots from trees of uniform age in a stand of *Pinus radiata*, Marks & Foster (1967) observed replacement of one mycorrhizal fungal associate by another. They believed their extensive anatomical observations indicated that mycorrhizas of a forest stand probably alter considerably during the lifetime of the stand.

Within 5 years of outplanting, Lamb (1979) noticed that *Pinus elliottii* plantations yielded up to 40 ectomycorrhizal species, while 20 different

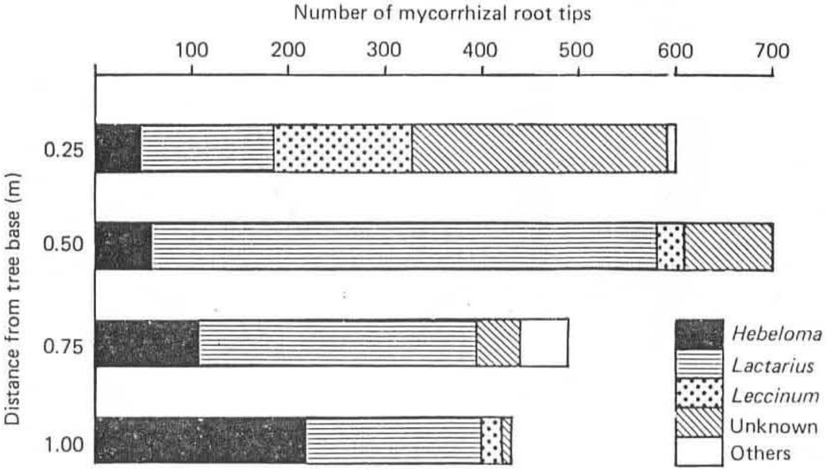

Fig. 5.4. Number of mycorrhizas of different types in 15 soil cores taken at increasing distances from the base of a *Betula pubescens* tree. (After Deacon *et al.*, 1983.)

Table 5.1. *Mycorrhizal formation on birch seedlings planted into unsterile soil supplemented with spores of 'early-' and 'late-stage' fungi.* (*After Fox, 1983*a)

	Per cent of mycorrhizas formed by inoculant fungus	Number of contaminant fungi
'Early-stage'		
Hebeloma sacchariolens	44	1
H. leucosarx	59	1
Inocybe geophylla	23	0
I. lacera	52	1
Laccaria proxima	67	1
L. tortilis	11	0
'Late-stage'		
Cortinarius delibutus	0	3
Lactarius pubescens	0	3
L. vietus	0	3
Leccinum roseofracta	0	3
Russula grisea	0	2

species were isolated from *Pinus radiata* stands of equivalent age. Similarly, Thomas, Rogers & Jackson (1983) revealed that in 2–4 years after outplanting Sitka spruce (*Picea sitchensis*) only E-strain mycorrhizas persisted from the nursery and the number of ectomycorrhizal fungi increased, such that in mature stands 24 different fungi were found.

An increased understanding of mycorrhizal changes in ageing stands is being achieved by the use of baiting techniques. Deacon *et al.* (1983) grew birch seedlings in soil cores taken from beneath fruit bodies of a range of ectomycorrhizal fungi. After 8–10 weeks, seedlings grown in cores from beneath fruit bodies of the 'early-stage' fungi *Laccaria* and *Inocybe* always developed mycorrhizas attributable to these fungi. In contrast, seedlings seldom or never developed mycorrhizas of the late-stage fungi *Lactarius* or *Leccinum*, although cores contained abundant mycorrhizas of both types. This demonstrates differences in the abilities of fungi which occur early and late in the sequence to establish mycorrhizas in field conditions, whereas in monoxenic culture both 'early-' and 'late-stage' fungi readily form mycorrhizas. Additional evidence for this distinction between early and late fungi is provided by Deacon *et al.* (1983) and Mason *et al.* (1983) using mycelial inocula, and by Fox (1983*b*) using basidiospores. Fox found that birch seedlings planted into basidiospore-amended, unsterile soil readily developed mycorrhizas with species of *Hebeloma*, *Inocybe* and *Laccaria* but not with *Cortinarius*, *Lactarius*, *Leccinum* or *Russula* (Table 5.1).

Table 5.2. *Mean number of root tips of different mycorrhizal types on birch seedlings grown in non-isolated and cored positions around a mature birch tree.* (*After Fleming, 1984.*)

Mycorrhizal type	Non-isolated	Cored
Lactarius	34^a	3^a
Inocybe, Hebeloma and *Laccaria*	20^a	50^a
Total mycorrhizal tips	54	53
Total root tips	61	82

Superscript refers to pairs in each row differing from each other at $P = 0.05$.

Clearly the observations have important implications for the selection of mycorrhizal fungi for inoculating into nurseries. The choice is dependent upon the position of the fungus in the succession, its ability to colonise roots in unsterile soil and its tolerance of the nutrient levels in the nursery soil. Further knowledge regarding the behaviour of mycorrhizal fungi in a variety of soil and environmental conditions is necessary in order to explain phenomena such as the replacement of *Hebeloma crustuliniforme* and *Laccaria laccata* inoculated onto Douglas fir seedlings by native mycorrhizal fungi within 5 months after outplanting onto dry, burned-over sites in the USA (Bledsoe, Tennyson & Lopushinsky, 1982).

So far we have mainly highlighted the events occurring in first-rotation forest plantations. The phenomena occurring under unmanaged forests or woodlands, where natural regeneration occurs in the understorey, may be different. Here we expect a stable and possibly declining microflora of mainly 'late-stage' fungi (Harvey *et al.*, 1976; Malajczuk, Molina & Trappe, 1982). In contrast to outplanted forest seedlings, the majority of the roots of regenerating tree seedlings appear to be infected with late-stage fungi such as *Lactarius*, *Cortinarius*, *Russula* and *Amanita*. Fleming (1983) suggested that a common feature of the late-stage fungi is the ability to form strands. When he planted axenically raised birch seedlings into soil in contact with the root system of a parent birch tree, late-stage *Lactarius pubescens* mycorrhizas formed on the seedling roots. However, where soil was isolated, by coring, from the parent tree roots and the characteristic mycorrhizal strands of late-stage fungi, the seedlings developed mycorrhizas of early-stage fungi and generally not those associated with *L. pubescens* (Table 5.2). Separation of these 'late-stage' fungi, like other root-infecting

Table 5.3. *Possible factors influencing the succession of mycorrhizal fungi on tree roots based on expected soil, fungal and host tree characteristics as viewed from* r–K *strategies*

	Stage of succession	
	Early	Late
Carbohydrate demand (supply by host tree)	Low	High
Available nutrients	In inorganic pool	Mainly in organic pool
Competitive ability of fungus	Due to rapid mycelial growth	Due to production of mycelial strands
Associations of mycorrhizal fungi with saprotrophic fungi	Competitive	Synergistic if not able to break down organic complexes, or competitive if mycorrhizal fungi are also decomposers

fungi, from a well-established food base appears to reduce their infection potential (Garrett, 1951; Fleming, 1983). These findings clearly raise interesting questions with respect to the roles of early- and late-stage fungi in forest plantations and in naturally regenerating woodlands, some of which will be explored in the next section.

Considerable evidence is thus now accumulating to support the concept of mycorrhizal successions on ageing trees, but what forces dictate changes in mycorrhizal associations? What physiological differences are there between 'early-' and 'late-stage' mycorrhizas?

Resources – their role in mycorrhizal succession

Some of the main changes occurring during the development of a forest stand are summarised in Fig. 5.1. A number of factors thought to be involved in determining mycorrhizal successions were proposed by Dighton, Harrison & Mason (1981), some of which are discussed here in the light of evidence in the literature (Table 5.3).

Carbohydrate requirement of ectomycorrhizas

The supply of carbohydrates (photosynthates) from the tree host to the fungal symbiont is of paramount importance to the development and functioning of mycorrhizas. This supply not only satisfies the energy and carbon demand for fungal growth but is intimately connected with nutrient uptake by mycorrhizal roots (France & Reid, 1983).

Table 5.4. *Growth of mycorrhizal fungi at three glucose levels (number of crosses is arbitrary scale of growth from 1 to 4 based on colony diameter on agar)*

	Glucose level		
	0.1 g l^{-1}	1.0 g l^{-1}	10 g l^{-1}
Hebeloma spp.	++++	++	+
Leccinum spp.	+	++	+++
Amanita muscaria	+	++	+++(+)

The requirement of light (and hence photosynthates) for mycorrhizal development was demonstrated by Björkman (1949) in pines where no mycorrhizal development was observed at 6% daylight but occurred only on nutrient-poor soils at 12% daylight and on all soils at 23% and 49% daylight. Hacskaylo (1973) discusses this and other evidence from trench plots, tree shading and phloem destruction in trees, to demonstrate the carbohydrate demand of the fungus from its tree host. The carbohydrate demand by mycorrhizal root systems can be very large. St John & Coleman (1983) cite figures for vesicular-arbuscular mycorrhizal plants equivalent to 1% of the total plant weight, or 6% of the weight of infected root can be accounted for by the carbon allocation to the fungus. This can be equivalent to 40–60% of the net photosynthesis. Both the increased fungal component (i.e. the sheath) of ectomycorrhizas and the production of large fruit bodies may be an even greater carbon drain on the tree. In one study Trappe & Fogel (1977) demonstrated that the fruit bodies of mycorrhizal fungi may require the carbohydrate equivalent of 1m^3 of spruce timber or as much as 25% of a tree's assimilate (Newman, 1978). Cultural experiments on solid media have shown that early-stage fungi are less glucose-demanding than late-stage fungi (Table 5.4), and that early-stage fungi produce small fruit bodies (*Laccaria*, 0.03 g dry weight/fruit body) compared with large late-stage fruit bodies (*Leccinum*, 5–10.5 g dry weight/fruit body) (Deacon *et al.*, 1983) and adds support to the possibility that early-stage fungi have a lower demand for, or reduced access to, host-derived carbohydrate.

An additional important feature of carbohydrate nutrition was demonstrated by Björkman (1960). He demonstrated interplant carbohydrate transfer when ^{14}C-labelled glucose injected into spruce and pine trees was detected in the achlorophyllous plant *Monotropa hypopitys* but not in the other sub-canopy vegetation. A common mycorrhizal fungal symbiont between the trees and *Monotropa* was implicated in this preferential carbon transfer. Interplant carbohydrate transfer between green plants has been shown by Reid & Woods (1969) using *Pinus taeda* seedlings of similar age in association with *Pisolithus tinctorius* and *Thelephora terrestris*. Where seedling trees were allowed to become connected by mycorrhizal hyphal bridges between root systems, ^{14}C applied as $^{14}CO_2$ to one of the pair was detected in the recipient plant from which $^{14}CO_2$ was excluded. No transfer was observed where hyphal bridges were not allowed to form.

With the potential for interplant transfer of carbohydrates and the probable increased carbohydrate demand by 'late-stage' fungi compared to 'early-stage' fungi, we can propose that one factor controlling the succession of mycorrhizas on trees is the ability of the photosynthetic capacity of the tree at different ages to satisfy the carbon demands of the array of fungi at any one time. Young trees may not have enough 'excess' photosynthate to support 'late-stage' fungi. In the experiments of Fleming (1983), seedlings planted into soil separated from the mother tree became mycorrhizal only with 'early-stage' fungi. Where the seedling birches were planted into soil not isolated from the mother tree's root system, late-stage mycorrhizal fungi were formed on the seedlings. This, we suggest, is possibly due to the fact that the late-stage fungi forming mycorrhizas on the roots of seedlings are also associated with a mother tree, thus they obtain their carbohydrates from the mother tree rather than from the seedling alone. This facility is an important consideration in comparing seedling survival under afforestation and natural regeneration. In afforestation programmes, the mycorrhizal fungi associating with the seedling trees will tend to be early-stage fungi (Chu-Chou, 1979; Lamb, 1979) derived from spore populations in the soil. In natural regeneration, however, it is possible that the dominant late-stage fungi may form mycorrhizal associations between existing mature trees and young seedlings by mycorrhizal strands (Fleming, 1983) and the carbohydrate flow from mature donor tree to recipient seedling may enhance seedling growth and mycorrhizal establishment even under severe shading conditions, a facility observed in vesicular-arbuscular mycorrhizas of *Plantago* sp. and *Festuca* sp. (Francis, 1983). Similar data exist for carbohydrate transfer from donor mother pine trees to recipient seedlings in naturally regenerating woodland (Read, 1985) and for inter-tree transfer of phosphorus and calcium (Woods & Brock, 1964) in mixed-aged mixed deciduous forests.

Evidence of changes in carbohydrate content or supply to roots with tree age is scant. Seasonal variation in sugar and starch contents of fine roots is expected to change according to photosynthetic rate and partitioning of end products to above- and below-ground biomass (Vogt *et al.*, 1980). Vogt *et al.* (1983*b*) suggested that fine root and mycorrhizal biomass fluctuate with stand development with maximum biomass at canopy closure and that nutrient-poor sites maintain a significantly higher mycorrhizal biomass than nutrient-rich sites, with trees on poor sites probably allocating a greater proportion of photosynthate to mycorrhizal production thereby satisfying mineral nutrient demands. In this manner the ageing stand would be able to sustain a most diverse mycorrhizal fungal flora around the time of canopy closure.

Table 5.5. *The effect of fertiliser on mycorrhizal development on* Pinus contorta *in Japanese Paper Pot culture*

	Percent mycorrhizal root tips		
	0.13 kg m^{-3} E[a] 11 ppm P	0.75 kg m^{-3} E 66 ppm P	1.5 kg m^{-3} E 132 ppm P
Non-mycorrhizal	0.18	0.1	0
Paxillus involutus	19.3	50.3	0.2
Hebeloma sacchariolens	55.0	16.4	0.4

[a] E = Enmag commercial fertiliser.

In addition to direct energy supply from the tree host for fungal growth, there are mutually dependent links between the supply of carbohydrates available for mycorrhizal development on root systems, the nutritional status of soil and the feedback to photosynthetic rates which have only recently been investigated (Marx, Hatch & Mendicino, 1977; France & Reid, 1983; Reid, Kidd & Ekwebelam, 1983). High levels of nitrogen and phosphorus in soil suppress the development of mycorrhizas on roots (Table 5.5). Marx *et al.* (1977) showed that the suppressed development of *Pisolithus tinctorius* on *Pinus taeda* was a result of decreased root sugar concentration, where sucrose concentration accounted for 85% of the variation in susceptibility of short roots to infection by *P. tinctorius* but fructose concentration was not correlated with infection. France & Reid (1983) produced a conceptual model of carbon and nitrogen interaction in ectomycorrhizal roots, where sucrose is immobilised in the fungus into storage forms, and nitrogen, primarily ammonium, is absorbed by the fungus and assimilated into amino acids in the sheath. When the host plant acts as a sink for nitrogen, amino acids are transported to the root tissue as glutamic acid and glutamine. Reid *et al.* (1983) demonstrated in experimental conditions with *P. tinctorius*-infected *Pinus taeda* that the percentage mycorrhizal infection and net photosynthesis increased with seedling age and that photosynthesis of mycorrhizal seedlings was greater than that of non-mycorrhizal seedlings. The addition of *P. tinctorius* or *Suillus granulatus* to *Pinus contorta* showed similar effects of increased net photosynthesis and biomass. Foliar analysis, however, suggested that phosphorus rather than nitrogen was responsible for the mycorrhizal seedling response. Increased photosynthesis as a result of mycorrhization is consistent with the ideas of source–sink relations in that the mycorrhizal fungus creates a carbohydrate sink and that both nitrogen and phosphorus concentrations, being enhanced by the presence of the mycorrhiza, could account for increased photosynthesis by, for example, increased chlorophyll concentration, decreased resistance to carbon dioxide diffusion, increased activity of carboxylating enzymes, and improved utilisation of assimilated carbon by sinks.

In terms of mycorrhizal succession on ageing trees, the carbohydrate supply may be an important determinant in the selection of mycorrhizal symbionts. An increased interdependence of the tree and symbiont for carbohydrate and nutrient dynamics with increased tree age would be consistent with the '*r*'–'*K*' concept. 'Early-stage' fungi exhibit rapid growth on simple media containing low levels of sugars (Table 5.4) and produce small fruit bodies. Late-stage fungi are more difficult to culture, requiring larger amounts of sugars and probably complex mixtures of vitamins which in nature they obtain from their tree host. This close dependence on the host tree and greater investment of energy resources into large fruit bodies and more persistent mycelial structures (strands) are consistent with '*K*' attributes.

Resource quality – a determinant of nutrient availability

As the forest stand ages, the resource quality of materials supplying nutrients to the trees decreases due to the increased tree-litter component containing a higher proportion of complex molecules (lignin and polyphenols). At canopy closure, temperature and moisture conditions become less favourable for decomposition (Swift, Heal & Anderson, 1979) and litter breakdown and mobilisation of mineral elements decline (Vogt *et al.*, 1983*a*) (Fig. 5.1). Rates of mineralisation become increasingly dependent on close-linked, nutrient-conservative cycling processes in the soil (Heal & Dighton, 1985). It is not surprising, therefore, to find the presence of mycorrhizas on seedlings to be favoured by mineral rather than organic soils (Alvarez, Rowney & Cobb, 1979) and mycorrhizas of mature forest associated with organic fractions (Harvey *et al.*, 1976). Under conditions of forest maturation the production of extracellular enzymes by mycorrhizal fungi would be an advantageous strategy in order to derive mineral nutrients and supplementary carbohydrates directly from organic sources. The development of close interrelations between decomposition and mycorrhizal roots could be hypothesised from the principles underlying '*r*–*K*' strategies (MacArthur & Wilson, 1967) as suggested by Went & Stark (1968) and Malloch, Pirozynski & Raven (1980). The 'direct cycling' hypothesis, generated by Went & Stark (1968) and based on observation from tropical forest floors, proposed that mycorrhizal fungi, in direct contact with dead plant remains, were able to act as decomposers. In this way it was possible for trees to extract mineral nutrients directly from decomposing litter and thus to circumvent the nutrient mineralisation pathway via saprotrophs. The arguments presented by Went & Stark were discussed in relation to further evidence by St John (personal communication) and Janos (1983). They suggested that although certain enzymatic capabilities are shown by mycorrhizal fungi which would enable them to enhance decomposition, the spatial distribution of mycorrhizal roots and hyphae in relation to decomposing litter and saprotrophic organisms may be of great significance in that they are in juxtaposition to localised sites of nutrient mineralisation.

Data supporting the direct cycling hypothesis, or indeed the idea that mycorrhizal fungi are involved in decomposition, are scarce and often conflicting. In experiments using trenched, dug and undisturbed forest soil plots under *Pinus radiata*, and in experimental systems, Gadgil & Gadgil (1971, 1975) demonstrated that there was competition between mycorrhizal and saprotrophic fungi which decreased the rate of decomposition of *P. radiata* litter. Where living mycorrhizal roots were excluded, 60–80% more weight loss of litter was recorded after 12 months (Gadgil & Gadgil, 1971). When this experiment was repeated under Scots pine (*Pinus sylvestris*) in Sweden (Berg & Lindberg, 1980), however, litter weight loss increases of 1–7% per 12 months could be attributed to removal of mycorrhizal roots from the system. Berg & Lindberg suggested that the magnitude of the effect may not be as great as that expressed by Gadgil & Gadgil and put forward a number of alternative suggestions to explain the results. Digging and sieving soil may present new energy resources to microorganisms, resulting in faster mineralisation. Removal of a nutrient sink (plant roots) may allow more nutrients to become available for the microorganisms, allowing higher turnover rates (similar competitive effects between roots and microorganisms were explored by Bosatta (1981)) and the formation of inhibiting substances in the soil. These are all possible alternative explanations for the observed effect.

The possession of enzyme capacity compatible with the hypothesis that

Table 5.6. *Acid phosphatase production by fungal mycelia in Hagem's medium with 10 ppm orthophosphate-P or inositol hexaphosphate-P after 42 days growth at 20 °C.* (After Dighton, 1983.)

	Phosphatase production (μg phenol mg^{-1} mycelium)	
Fungus	orthophosphate-P	inositol hexaphosphate-P
Hebeloma crustuliniforme	29.8	23.9
Lactarius rufus	26.3	22.2
Paxillus involutus	17.1	10.2
Lactarius pubescens	12.8	7.6
Amanita muscaria	5.8	8.8
Suillus luteus	5.0	9.2
Marasmius androsaceus (s)	20.0	1.7
Mycena galopus (s)	0.9	0.2

(s) = saprotrophic fungus, the remainder are mycorrhizal.

Table 5.7. *Release of PO_4-P from 10 ppm inositol hexaphosphate (IHP) in Hagem's medium by fungi grown in liquid culture at* 20 °C. (After Dighton, 1983.)

Fungus	P released (μg P mg^{-1} fungus)	Percent P release from IHP and retained in fungus
Lactarius rufus	86.1	9.2
Paxillus involutus	62.4	16.7
Suillus luteus	7.1	92.5
Mycena galopus (s)	13.4	76.7
Marasmius androsaceus (s)	2.7	34.0

(s) = saprotrophic fungus, the remainder are mycorrhizal.

mycorrhizal fungi express *K*-strategist attributes is documented in the literature. Bartlett & Lewis (1973) demonstrated phosphatase and phytase activity of mycorrhizal beech (*Fagus* spp.) roots, although surface contamination by rhizosphere microflora may have complicated the interpretation. Similar information on phosphatase production by excised roots is available from spruce (Alexander & Hardy, 1981). The phosphatase capacity is a facility of the fungal partner, as demonstrated in pure cultures (Ho & Zak, 1979; Dighton, 1983) and the production may be greater than that of recognised saprotrophic basidiomycetes (Table 5.6). Dighton (1983) also demonstrated a greater orthophosphate production as a result of hydrolysis of inositol hexaphosphate by pure cultures of mycorrhizal fungi than could be utilised by fungal growth (Table 5.7). This phenomenon was also observed by Bartlett & Lewis (1973) and may be important in terms of supplying phosphorus to the tree host from organic sources.

A number of mycorrhizal fungi are shown to produce polyphenoloxidases (Giltrap, 1982), particularly species of *Lactarius*, which tend to be unspecialised facultative mycorrhizal fungi with a broad host range. Cellulase activity by mycorrhizal fungi is also documented; Oelbe (1982), following the work of Norkrans (1950), demonstrated cellulolytic activity of mycorrhizal varieties of *Tricholoma aurantium*. Similarly high cellulase activity of mycorrhizal *Salix rotundifolia* roots was reported by Linkins & Antibus (1981) and by St John (personal communication). It is interesting here that the mycorrhizal strands have a higher exocellulase activity than the mantle (60 and 140 times greater activity of exocellulase and β-glucosidase, respectively). *S. rotundifolia*, growing in Arctic tundra, may well rely on its mycorrhizal fungi for litter decomposition and nutrient release due to the short active season for decomposition. If this is so it would be in agreement with adaptive strategies for stressed environments (adversity selection) according to the '*r*'–'*K*'–'*A*' matrix of Southwood (1977) (Heal & Dighton, 1985). In semi-aseptic culture, *Suillus luteus* in association with *Pinus contorta* seedlings significantly increased the decomposition of cellulose (cotton) and chitin (Latter & Dighton, personal communication).

Work in culturing mycorrhizal fungi to examine their enzyme capabilities and their acquisition of nutrients and carbohydrates from organic sources (Lundeberg, 1970; Hacskaylo, 1973) may provide some information on the physiology of the mycorrhizal fungi. The demonstration of these physiological capabilities in a wide variety of fungi from early, mid, and late successional stages, in conjunction with the host root tissue, is, however, much needed in order to understand fully the physiological basis of succession.

Discussion

Changes in the structure of above-ground plant communities during ecosystem succession or the development of forest stands can be seen to influence the mycorrhizal flora. The mechanisms of change in mycorrhizal dynamics is far from obvious, changes in carbohydrate supply from the host tree and increasing recalcitrance of forest floor organic matter are two major factors which might influence successional changes of mycorrhizal flora. Evidence that the change in mycorrhizal fungi is of a successional nature is strong, with similar patterns of fruit bodies occurring sequentially with age in a number of tree species (Lamb, 1979; Chu-Chou & Grace, 1981, 1983; Deacon *et al.*, 1983; Last *et al.* 1983). Of the little that is known regarding the differences in the physiology of the fungi during succession, a number of tentative hypotheses show them to have characteristics predicted by the '*r*'–'*K*'–'*A*' model of Southwood (1977). 'Early-stage' fungi have a low carbohydrate demand for rapid growth and, as a result, many 'nursery' species (e.g. *Thelephora terrestris*) are not competitive after outplanting into nutrient-poor soils but are highly so in the very fertile soils of the nursery which may often be fumigated before seeding. The formation of mycelial strands by many of the 'late-stage' fungi may be seen as evidence of long-lived structures with a longer turnover time (*K*-characteristics *sensu* MacArthur & Wilson, 1967), along with the potential for litter decomposition by exoenzymes supplementing carbohydrate and mineral nutrient demand in later stages of forest development (Giltrap, 1982; Oelbe, 1982; Dighton, 1983), particularly where unfavourable environmental conditions exist, tending to select for '*A*'-strategies (Southwood, 1977; Linkins & Antibus, 1981).

What benefit is there in looking for the physiological factors behind mycorrhizal successions? Where man wishes to intervene and attempt to enhance tree growth by the artificial inoculation of forest seedlings with mycorrhizal fungi, a correct choice of fungus is necessary to optimise growth and survival of the seedlings and persistence of the introduced fungal strain. In first-rotation forestry the choice of effective strains of early-stage fungi for the appropriate soil type and climatic zone appears to be essential (Mason *et al.*, 1983). We have seen that late-stage fungi cannot successfully compete with early-stage fungi under such conditions, while other mycorrhizal fungi may have a limited effective climatic tolerance. *Pisolithus tinctorius*, for example, has proved to be a very successful mycorrhizal fungus on a number of sites in the southern USA (Marx, 1980), but appears to be ill adapted to cooler conditions (Momoh & Gbadegesin, 1980; Grossnickle & Reid, 1983) where indigenous, and therefore more ecologically adapted, fungi appear to perform better. In second-rotation forests the indigenous mycorrhizal flora on roots of cut stumps will consist mainly of late-stage fungi. Their influence on the mycorrhizal flora of newly planted seedlings has yet to be evaluated, but second-rotation decline in some parts of the world may, in part, be due to the availability of a restricted and rather host/age-specific mycorrhizal flora (Robinson, 1973; Malajczuk *et al.*, 1982). In the UK, however, the small scale of the landscape and size of plantations would allow the maintenance of a broad spectrum spore population at all times, thus second-rotation decline due to a depauperate mycorrhizal flora would not be expected. In naturally regenerating woodlands, on the other hand, the predominance of late-stage fungi might be more beneficial to seedling trees than early-stage fungi. In such situations the possibility of carbohydrate transfer from mother trees to seedlings via mycorrhizal bridges may be of benefit to seedlings growing in sub-optimal light conditions on the forest floor. Can any similar advantage occur in clear-cut areas? If mycorrhizal fungi are still viable on roots of cut stumps they may act in a similar manner to benefit second-rotation trees by the transfer of carbohydrates and mineral ions as a result of saprotrophic activity of the fungus at the stump end.

A number of questions have been raised by this discussion of the physiological basis for the succession of mycorrhizal agarics in relation to resources available to them. Their implications are broad ranging in the selection of mycorrhizas for optimisation of forest tree growth. These questions, we feel, are the challenge for future mycorrhizal research.

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